Diving behaviour in two distinct populations of gravid Flatback turtles *Natator depressus*

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ABSTRACT

This paper presents the first data on the diving behaviour of Flatback turtles, *Natator depressus*, between nesting events. Dive profiles were recorded in turtles from breeding populations at Curtis Island in Queensland and at Bare Sand Island in the Northern Territory, using Time-Depth Recorders (TDRs). Both populations displayed dive types typical of those described in other internesting sea turtles. Dives spent on the seabed were most prevalent, accounting for 57% of the time at depth. While on the sea bed, the turtles apparently remained inactive, cyclical changes in depth reflecting the tidal cycle. These inactive dives were long compared to those typical of other large sea turtles such as *C. mydas* and *C. caretta*, up to 98 min (mean 80±12 min), and with a mean and median of 50 and 52 min, respectively. In both populations, these dives occurred more commonly by day, by an average of 14%, and were most prevalent in the middle third of the internesting interval in most turtles, while the eggs were maturing. The turtles spent only 10% of their time at or near the surface and surface intervals rarely exceeded a few minutes, insufficient to be attributed to a need for either rest or thermoregulation. The Bare Sand Island population showed longer dive durations and proportionally more dives with a gradual ascent phase, a phase presumed to be a method of compensating for buoyancy loss and a way for turtles to conserve energy in mid-water while still moving around. Maximum dive depths of 29 m and 44 m were recorded at Curtis Island and Bare Sand Island respectively, probably reflecting differences in bathymetry.

Key words: diving, flatback, *Natator depressus*, internesting, dive duration

Introduction

The availability of Time-Depth Recorders (TDRs) offers opportunities to infer information about specific behaviours of turtles over long periods. Sea turtles normally nest more than once within the same nesting season (Hirth 1980) and the period between nesting events, the internesting interval (Limpus 1985), is spent primarily preparing the next clutch of eggs for laying (Miller 1985). Sea turtles commonly do not feed at this time (Carr *et al.* 1974; Bjorndal 1985; Tanaka *et al.* 1995; Limpus et *al.* 2001; Hays *et al.* 2002a) and, therefore, behaviours which conserve energy may be at a premium. Indeed, many sea turtles spend the majority of the internesting interval apparently inactive on the seabed, sometimes referred to as resting (van Dam and Diez 1997), surfacing only briefly to breathe (Starbird *et al.* 1999; Hays *et al.* 2000a, 2002b; Houghton *et al.* 2002).

Dives with a slow gradual ascent phase, which may be reptilian-specific (Hochscheid *et al.* 1999), are also often believed to occur in conjunction with energy-conserving behaviour and have been recognised in some species (Minamikawa *et al.* 1997; Hochscheid *et al.* 1999; Houghton *et al.* 2002). During the gradual ascent phase the turtles have been found to be at or near neutral buoyancy (Minamikawa *et al.* 1997; 2000), at which time they are believed to be compensating for the loss of buoyancy. When slowly ascending, the remaining lung air expands, increasing buoyancy, and in so doing compensates for the buoyancy loss due to metabolism (Minamikawa *et al.* 2000). It has been suggested that these dives, described extensively in sea snakes (Rubinoff *et al.* 1986; Graham *et al.* 1987), are favoured during periods of travelling as a way of conserving energy (Hochscheid *et al.* 1999; Houghton *et al.* 2002) and it is known that these dive types are used by Green turtles, *Chelonia mydas,* undertaking oceanic migrations to their nesting beach (Hays *et al.* 2001). Also, a recent study measuring turtle activity revealed that in most of these dives *C. mydas* swam at least some horizontal distance while at the same time slowly ascending (Hays *et al.* 2004).

In addition to either sitting on the sea floor or slowly ascending in mid-water, a third possibility for conserving energy during the internesting interval is for turtles to stay inactive at the surface (Sapsford and van der Riet 1979). This behaviour has been suggested to be a form of surface 'basking' (Sapsford and van der Riet 1979), where a possible increase in body temperature due to solar radiation may in turn increase the rate of egg production (Whittow and Balazs 1982; Limpus *et al.* 1994). However, there is no good evidence that sea turtles warm themselves by 'basking' at the surface Sato *et al.* 1995; Read *et al.* 1996) so time spent at the surface, if it occurs, could be associated with resting. There are some observations that 'basking' could be more common in *N. depressus* than in other sea turtles (Cogger and Lindner 1969; Bustard 1972).

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N. depressus differs from other sea turtles in that it is restricted to the continental shelf of Australia and southern New Guinea (Walker and Parmenter 1990). They breed only on Australian beaches (Limpus *et al.* 1988) and lack the post-hatchling oceanic dispersal phase seen in other sea turtles (Walker and Parmenter 1990). The present study describes the normal dive behaviour between nesting events for *N. depressus*. An important aspect of the study was to determine typical dive depth and durations, as such information is lacking for *N. depressus*. The species is seldom known to dive deeper than 40-45 m (Walker 1991; Poiner and Harris 1996; Robins and Mayer 1998), while dive durations are unknown. Data suggest that *N. depressus* survive forced submersion better than other sea turtle species caught accidentally by trawlers (Poiner *et al.* 1990). For instance, *N. depressus* has a mortality rate of 11% in the northern Australian prawn fishery in comparison to 22% for Loggerhead turtles, *Caretta caretta* (Poiner and Harris 1996). We therefore hypothesized that *N. depressus* would show comparatively longer dive durations to most other sea turtles, which are commonly less than 30-40 min, and rarely more than an hour (*Dermochelys coriacea*: Eckert *et al.* 1986; Wallace *et al.* 2005; *Lepidochelys kempii*: Mendonca and Pritchard 1986; *Caretta caretta*: Sakamoto *et al.* 1990a; 1990b; Lutcavage and Lutz 1991; Houghton *et al.* 2002; *C. mydas*: Brill *et al.* 1995; Hays *et al.* 2000; 2001), reflecting a respiratory physiology particularly suited to sustain prolonged shallow dives (Sperling *et al.* 2007).

Dive durations may further be influenced by body size, with maximum durations being positively correlated with body size. While this relationship is well documented in endotherms, the same interspecific relationship fails to show up in ectotherms but may still be evident within a species (Brischoux *et al.* 2008). In the present study, data are presented on the diving behaviour of *N. depressus* from two different breeding populations. One population is part of the eastern, central Queensland breeding stock, which is genetically and physiologically discrete (Limpus *et al.* 1993; Dutton *et al.* 2002) from the other that breeds in the Northern Territory. The turtles at Curtis Island are larger, with an average curved carapace length of 92 cm compared to 86 cm at Bare Sand Island (Limpus 1971; Whiting and Guinea 2006). We therefore hypothesize that Curtis Island turtles dive for longer to similar depths. The two populations are also likely to encounter different bathymetry, with the area used by turtles nesting at Curtis Island being considerably shallower than around Bare Sand Island (Sperling 2007). We hypothesized that dives to the seafloor, as in dive type 1, may be favoured in shallow water, while mid-water dives may be favoured in deeper water where the seafloor may be less accessible.

Material and methods

Study sites and animals used

The present study is based on ten individuals at Curtis Island, Queensland (23°45'S, 151°17'E) and ten individuals at Bare Sand Island, Northern Territory (12°32' S, 130°25' E). Each individual was tracked for one internesting interval, with one turtle tracked for two consecutive intervals. The internesting interval is the time between the end of one successful nesting event and the following attempt, whether successful or not (Limpus 1985). Curved Carapace Length, CCL, was measured on all turtles at each encounter (Table 1). The turtles studied at Curtis Island were 95.6 ±2.2 cm long, which is significantly bigger ($P<0.001$, *t*-test) than the turtles at Bare Sand Island (87.1 ±2.8 cm). The two study sites are 2700 km apart. Curtis Island is a 45 km long island outside Gladstone, with a 5 km nesting beach at the south-eastern end. Bare Sand Island, an uninhabited sandy island with a total perimeter of 1.8 km, is situated 50 km west of Darwin in Fog Bay. The two populations differ in nesting season, with the Queensland population breeding between October and January (Limpus *et al.* 1984) and the Northern Territory population nesting between March and November (Guinea 1994). The study was conducted during the nesting seasons of 2000/01 and 2001/02 at Curtis Island and during the nesting season of 2001 at Bare Sand Island. Nightly patrols on the nesting beach made sure that all experimental turtles were intercepted.

Recording of dive profiles

Two types of Time-Depth Recorders (TDRs) were used to record dive profiles, both of which record and store *in situ* depth and temperature information. Lotek LTD_100 loggers (Lotek Wildlife Monitoring, Canada) were used together with a specially made housing (Les Fletcher, University of Queensland) and logged the depth every 6 s with an accuracy and resolution of 1.1 m and 0.09 m, respectively. The second TDR used was Minilog 8-Bit TDR (Vemco Limited, Nova Scotia, Canada) which logged depth every 45 s, with an accuracy and resolution of 1.0 m and 0.2 m, respectively. At Curtis Island, five deployments were made with Lotek loggers and five with the Vemco loggers, and all but two of the deployments, the two experiencing battery failure prior to interval completion, resulted in data collected from complete internesting intervals. At Bare Sand Island eight deployments were made with Lotek loggers and three with Vemco loggers. Two deployments were made on the same individual, and all deployments resulted in data collected from complete internesting intervals.

For all except five turtles the TDRs were attached under the rear marginal scutes of the carapace using a stainless steel bolt, washers and nylon threaded nut, following the procedure designed originally by Sally Hopkins-Murphy (South Carolina Department of Natural Resources). The hole was drilled while the turtle was on its back, using a battery-operated drill. The attachment method was trialled on a captive turtle (Sea World, Gold Coast) before any field work, and no contraindications emerged. The last five turtles, two at Curtis Island and three at Bare Sand Island, had a satellite transmitter attached as well. In these cases, both instruments were bolted to a plate which was secured to the turtle's carapace using a special six-strap harness (Sperling and Guinea 2004).

Table 1. The occurrence of the various dive types and the duration of dive type 1a and dives with a gradual ascent phase (3, 4, b4, s4). CCL is 'Curved Carapace Length', a standard measurement along the midline of the carapace.

Tag	CCL	At	Dive type (% of dive-time)									Duration type 1a (min)			Duration gradual ascent (min)		
#	(cm)	surface	1a	1b	2	3	4	d4	s4	5	Unident.	mean	median	max	mean	median	max
Curtis Island																	
K18551	92.7	6.1%	64.7%	14.7%	0.9%	3.4%	3.2%	1.4%	0.4%	0.2%	11.2%	39.6	39.8	64.5	21.7	20.3	44.3
K19901	95.1	7.6%	70.2%	17.6%	1.2%	0.1%	1.4%	0.4%	0.8%	0.4%	7.8%	40.0	41.0	60.1	10.5	9.6	25.3
K20172	98.2	7.5%	56.8%	18.9%	0.7%	0.2%	3.5%	2.2%	4.4%	0.1%	13.2%	56.8	57.4	87.0	28.3	27.8	61.5
T15865	92.7	11.0%	57.0%	21.2%	1.2%	0.4%	4.1%	1.3%	1.5%	0.1%	13.1%	45.4	48.0	74.3	15.1	13.5	38.3
T20906	97.6	6.5%	72.0%	16.7%	0.6%	0.3%	2.4%	1.1%	1.3%	0.2%	5.4%	51.7	51.3	89.4	11.4	10.6	32.1
T74180	97.1	9.7%	42.1%	26.3%	1.9%	1.3%	2.7%	1.3%	1.3%	0.6%	22.5%	47.4	50.3	95.3	12.6	12.8	47.3
T74203	96.6	15.9%	50.1%	22.7%	0.6%	0.5%	3.4%	3.9%	1.7%	1.6%	15.5%	35.0	34.9	84.0	14.9	14.0	41.4
T97155	95	7.9%	83.7%	10.9%	0.5%	0.1%	0.7%	2.6%	0.2%	0.0%	1.3%	38.8	38.5	64.3	16.5	15.8	31.1
T97203	95.2	6.3%	63.9%	19.7%	0.2%	2.1%	2.8%	1.5%	0.8%	0.2%	8.8%	37.8	39.8	63.8	16.2	15.8	48.0
T97213	92.2	6.8%	49.2%	21.8%	0.4%	1.7%	3.9%	3.7%	4.7%	0.1%	14.6%	57.1	58.8	98.4	31.3	33.2	63.1
Mean	95.2	8.5%	61.0%	19.1%	0.8%	1.0%	2.8%	1.9%	1.7%	0.3%	11.3%	45.0	45.9	78.1	17.9	17.3	43.2
Bare Sand Island																	
K 19215	87.4	11.1%	46.5%	8.1%	0.2%	1.0%	14.3%	6.9%	8.5%	0.8%	13.7%	56.0	59.2	80.3	35.9	42.3	62.2
K 19278	85.4	15.2%	58.4%	12.9%	0.7%	0.5%	9.9%	4.6%	5.5%	0.8%	6.7%	52.5	54.4	81.7	18.6	15.6	54.9
K 26302	88.5	16.6%	22.2%	4.8%	2.6%	0.9%	19.5%	3.7%	8.1%	1.6%	36.7%	46.5	48.0	62.3	19.3	18.0	48.8
K 29001	87.8	18.1%	44.1%	14.1%	0.8%	3.3%	16.2%	5.0%	6.3%	1.5%	8.7%	46.3	51.1	79.6	27.3	26.7	62.5
K 45837	82.4	13.1%	64.7%	6.9%	1.8%	0.7%	9.1%	3.9%	3.8%	2.2%	7.0%	43.5	45.0	72.8	29.9	27.4	58.5
K 45918-1	87.9	9.6%	58.3%	5.5%	0.4%	1.0%	15.6%	8.7%	5.9%	0.7%	3.9%	57.9	62.3	92.3	39.5	40.5	72.8
K 45918-2	-	7.6%	77.9%	7.6%	0.4%	0.6%	5.4%	3.2%	1.1%	0.4%	3.5%	53.6	57.5	80.1	23.3	22.8	49.5
K 45978	87	6.2%	57.2%	15.9%	0.0%	0.0%	2.8%	4.7%	13.8%	1.2%	4.5%	57.8	62.2	86.0	34.0	35.6	64.3
K 7960	90.8	11.1%	50.8%	17.5%	1.0%	0.2%	5.6%	2.9%	4.3%	0.8%	16.8%	54.1	56.4	80.7	19.6	19.7	49.3
T 94222	83.3	10.9%	67.1%	11.7%	0.1%	0.0%	2.9%	2.5%	6.8%	2.3%	6.6%	69.0	72.9	95.9	30.0	34.1	48.7
T 94333	90.7	9.1%	47.0%	21.3%	0.2%	0.0%	5.6%	5.1%	8.7%	0.4%	11.7%	61.6	64.1	95.7	23.2	21.6	50.9
Mean	87.1	11.7%	54.0%	11.5%	0.7%	0.8%	9.7%	4.6%	6.6%	1.2%	10.9%	54.4	57.7	82.5	27.3	27.7	56.6

Categorisation of dive profiles

Data from the TDRs were downloaded to a computer for analysis. Depth corrections of up to 0.5 m were made to account for drift in sensitivity, determined by calibration, i.e. each TDR was lowered into the sea to various known depths before and after each deployment. Initial analyses was made using a custom-written dive-analysis program (M. Gordos, Visual Basic, Microsoft Corporation©). The program produced a list of dives; each dive defined as a series of consecutive recordings below a certain threshold depth. Choice of threshold depth took into consideration the possibility of turtles breathing at the surface in a fully vertical position, together with the resolution and accuracy of the loggers. Because attachment was at the rear of the turtle, approximately 1 meter from the head, depths recorded below 2.0 meters for deployments of both Vemco and Lotek TDRs were judged to indicate a dive. For turtles with harnesses, the loggers were situated about 0.5 m further up their carapace, and for these turtles depths below 1.5 m were considered indicative of diving.

Despite great variability in the dive patterns seen, many of the individual dives could be sorted into categories based on the shape, depth and duration, most of which matched dive-types defined already in the literature (Fig. 1) (Minamikawa *et al.* 1997; Hochscheid *et al.* 1999; Hays *et al.* 2000; 2002b; Houghton *et al.* 2002). These were not necessarily mutually exclusive, but were useful to allow interpretation because they appear to represent different types of behaviour. Each dive, as defined by the custom-written dive-analysis program, was examined and then classified subjectively into a dive type based on profile shape and the depth and duration of the dive. To prevent any bias, data sets were looked at in random order without any prior knowledge of patterns at the corresponding study site. The differences in spatial and temporal scales for the two TDRs did not appear to influence the resulting dive categories. However, more of the data attained with Vemco loggers had to be excluded from further analysis because of their poorer depth resolution.

Before classifying the dives, some patterns identified erroneously as dives by the dive-analyses program were subtracted from the total number of dives for each turtle. As the program would count measurements below the threshold depth of 2.0 or 1.5 meters as a dive, 'false' dives would easily be recorded when turtles stayed around this depth, resulting in a series of apparent dives and surface events measured slightly below and above the threshold depth, respectively. Also, the shallow threshold depth could lead to subsurface swimming with periodic breaths being counted as single dives. However, it is believed that error from this source was minimised by excluding short dives (12 s or less for Lotek loggers or 45 s for Vemco loggers) which were shallower than 3 meters, and longer dives when the depth difference between the pre-dive surfacing event and the dive was less than 1 meter unless the profile confirmed a single definite dive. The remaining dives were then classified into dive types 1a, 1b, 2, 3, 4, s4, d4, 5 or 'unidentified', as follows (Fig. 1):

Dives of type 1a, described by Minamikawa *et al.* (1997) and Houghton *et al.* (2002) and similar to the 'U-dives' described by Hochscheid *et al.* (1999), Hays *et al.* (2000; 2002b) and Reina *et al.* (2005) show a rapid descent, a long bottom time and a rapid ascent (Fig. 1). They frequently show a tidal pattern. The dives are assumed to be dives in which the turtles spend time inactive on the sea floor (Hays *et al.* 2004) and they have therefore been referred to also as 'resting dives' (van Dam and Diez 1997) although *C. mydas* nesting on Cyprus have been found to forage actively during 'U-dives'. In the present study, only dives with the described time-depth profile longer than 10 min and with at least 75% of the bottom phase following the expected tidal pattern were classified as dive type 1a.

Dives of type 1b are similar to 1a in profile but, instead of having a period of apparent inactivity at the bottom, the bottom phase shows some changes in depth indicating activity. Houghton *et al.* (2002) made a similar distinction between dives with a flat bottom phase (1a) and a more erratic (variable depth) bottom phase (1b).

Dives of type 2, described by Minamikawa *et al.* (1997) and Houghton *et al.* (2002), and similar to the 'V-dives' described by Hochscheid *et al.* (1999), Hays *et al.* (2004) and Reina *et al.* (2005), show a steep descent followed by an immediate steep ascent (Fig. 1). These dives have been suggested to be exploratory in nature (Hochscheid *et al.* 1999).

Dives of type 3, as described by Minamikawa *et al.* (1997) and described as dive type 1 by Hays *et al.* (2001) resemble the dives described as 'shallow travelling dives' by Hochscheid *et al.* (1999). They consist of a quick descent followed by a gradual ascent phase and then a quick return to the surface (Fig. 1). The slow gradual ascent phase is thought to be the result of the turtle compensating for loss of buoyancy as lung volume decreases (Minamikawa *et al.* 2000). These dives may be favoured during periods of travelling as a way of resting in mid-water (Hochscheid *et al.* 1999; Houghton *et al.* 2002).

Dives of type 4, as described by Minamikawa *et al.* (1997) and described as dive type 2 by Hays *et al.* (2001) are similar to those described as an 'S-dive' by Hochscheid *et al.* (1999). They consist of a quick descent followed by a quick first ascent; the turtle then apparently stops at a certain depth, sometimes referred to as a 'dive stop' (Hochscheid *et al.* 1999) where it ascends gradually for a while before returning to the surface in a final quick ascent (Fig. 1). As in dive type 3 the slow gradual ascent phase is thought to be the turtle compensating for loss of buoyancy, where the 'dive stop' is dependent on the lung volume, so as to make the turtle at or near neutral buoyancy (Minamikawa *et al.* 1997; 2000).

Dive type s4 is a newly described dive type from this study (Sperling 2008). These dives resemble dive type 4, but have, in addition, 'spikes' in the gradual ascent phase, i.e.

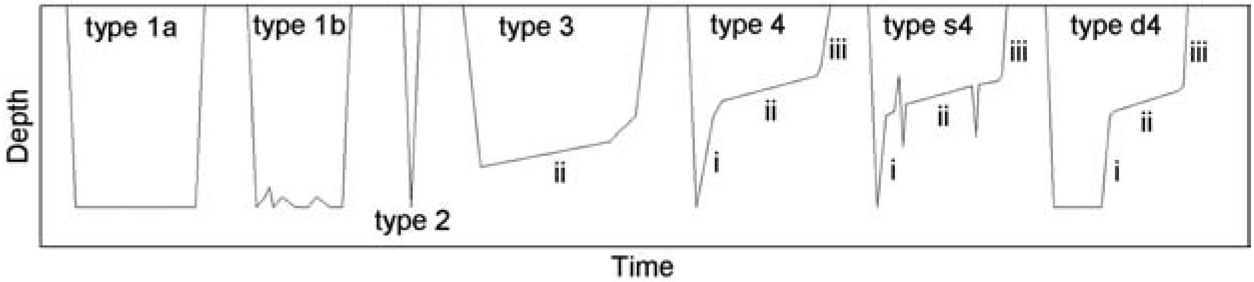


Figure 1. The dive types as described here shown schematically. Terminology commonly used for dives with a gradual ascent phase includes first ascent (i), gradual ascent or dive stop (ii) and final ascent (iii).

additional trips to deeper and/or shallower water. They are suggested to be relatively active compared to dive type 4, and may indicate a turtle spending time actively exploring the water column (Sperling 2008).

Dive type d4 is also a newly described dive type from this study (Sperling 2008). These dives resemble dive type 4 but the initial descent is followed by some time spent at the deepest part of the dive. They are suggested to stem from the turtle staying on the seabed as in dive type 1a, before initiating a gradual ascent phase, and may therefore be relatively inactive. The vertical distance travelled from the seabed to the point where the gradual ascent phase is initiated may be indicative of the change in lung volume from oxygen consumed during the bottom phase (Sperling 2008).

Dives of type 5 resemble type 5 dives described by Houghton *et al.* (2002) and the 'subsurface dives' described by Hochscheid *et al.* (1999) which are thought to indicate near-surface activity. In the present study these dives are no deeper than 3 meters, last longer than 12 or 45 s (for dives recorded with Lotek and Vemco loggers, respectively), and do not fit any of the above categories.

Statistical analysis

Mean is given for most variables to allow for comparisons with other studies, and median values are given also for some variables where these are thought to give a more informative representation of the prevalent behaviour. When mean values are given, they are presented with 1 SD. Comparisons between the two populations were made using Student's *t*-test on means. Correlations within individual turtles for dive durations, depths, surface durations etc. were explored using linear regressions. Partial regressions were used to test for the effect of turtle size on dive duration. SigmaStat™ Statistical Software (v2.03) and SPSS© for Windows (10.0.1) were used for analyses.

Results

Time underwater, at the surface, and relative occurrence of different dive types

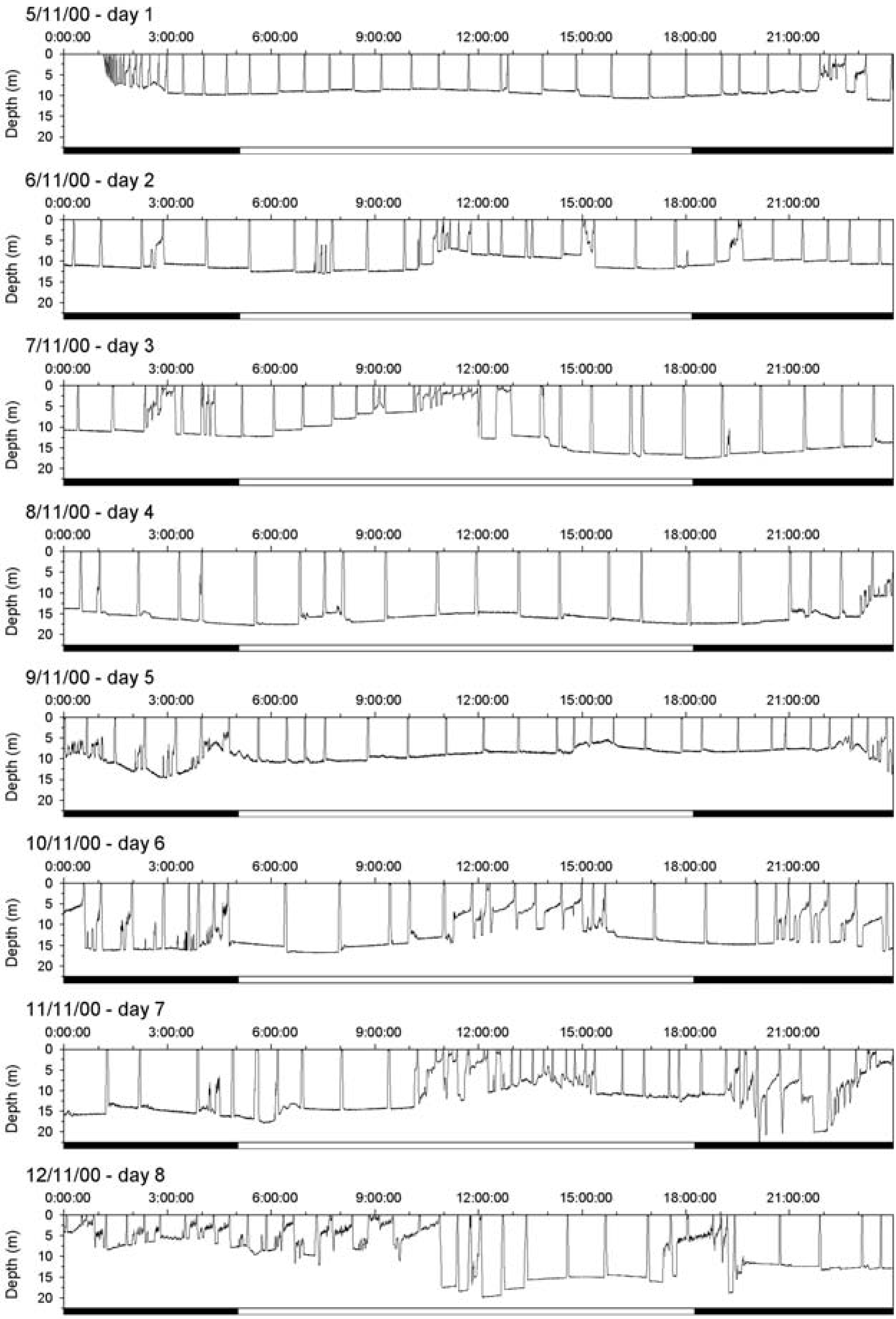
All the turtles spent most of their time at depth, with little time (10 ±4%) at or near the surface (Table 1). Average time spent diving, i.e. below the threshold depth (1.5 or 2.0 m) and referred hereafter to as 'dive-time', was 91.5 ±3.0% and 88.3 ±3.7% for Curtis Island and Bare Sand Island, respectively. Only one turtle (T15865) spent considerable time at the surface on two consecutive days, with depth measurements staying consistently around 0 m for several hours in the middle of each day. The turtles at Curtis Island (n=10) averaged 1.9 ±0.4 min at the surface between dives, significantly ($P=0.008$, power of test 0.772, *t*-test) less than the 2.4 ±0.5 min for turtles at Bare Sand Island (n=11). Although turtles carrying Vemco loggers frequently showed a longer surface duration, probably due to the greater sampling interval, the choice of TDR did not affect the average surface duration ($P=0.289$, *t*-test).

Each turtle showed a variety of profiles, with dive type 1a dominant in all individuals (Table 1). While dives of type 2, 3 and 5 occurred negligibly in both populations, the turtles at Curtis Island spent significantly more dive-time engaged in dive type 1b ($P=0.016$, *t*-test) with 19.1% compared to 11.5% for the Bare Sand Island population. In contrast, the turtles at Bare Sand Island spent more time engaged in the various type 4 dives (4, s4 & d4) with 21.0% compared to 6.5% of the dive-time for the Curtis Island turtles ($P<0.001$, *t*-test). A full profile is shown for turtle T97213 (Fig. 2).

Variations in dive depth and duration

The maximum dive depth for turtles was 29 meters at Curtis Island and 44 meters at Bare Sand Island, with dives of 20 m or less being most common at both study sites. Generally dives were as expected deeper for Bare Sand Island turtles (Fig. 3). In most cases the deeper dives were dive type 1a, with some dive types 2 and 4 reaching similar depths. Most of the turtles showed only a few dives around the maximum depth and, in addition, have one or two modal depths for dive type 1a, resulting in a variety of depth distributions (Fig. 4).

N. depressus showed some long dives, the longest being 98 min. However, most of the dives were short. Dive duration varied with the type of dive, where type 1a was usually also the longest of the dive types. Dive type 1a was on average about 10 min longer ($P=0.011$, power of test 0.713, *t*-test) for Bare Sand Island turtles compared to Curtis Island turtles, while the maximum dive durations were similar (Table 1). The descent and ascent part of these dives usually lasted only between 1 and 3 min, even for the deepest dives. Dive durations for dive types 1b, 2 and 5 were similar for the two populations, while turtles



5/11/00 - day 1

6/11/00 - day 2

7/11/00 - day 3

8/11/00 - day 4

9/11/00 - day 5

10/11/00 - day 6

11/11/00 - day 7

12/11/00 - day 8

Figure 2.

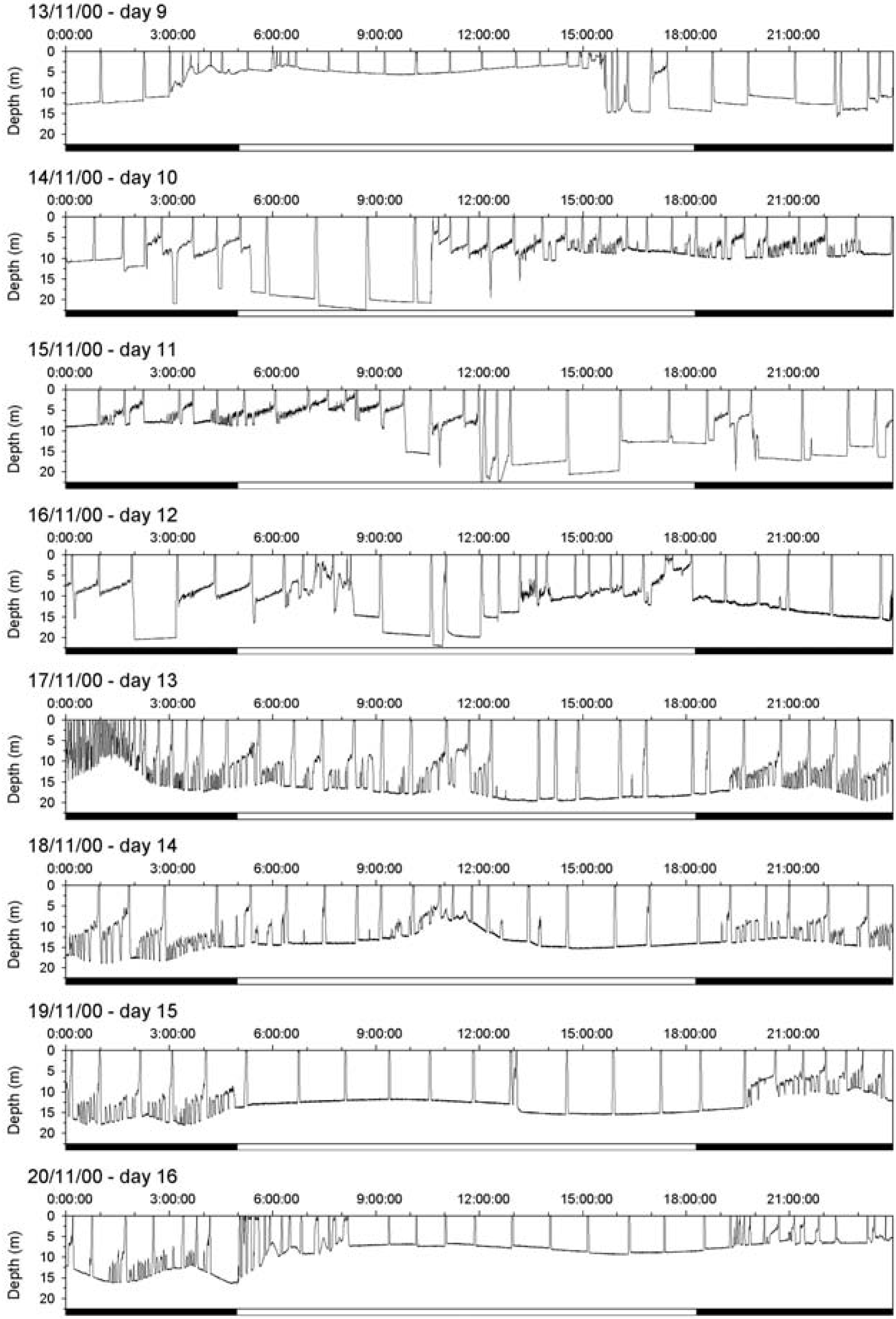


Figure 2. continued

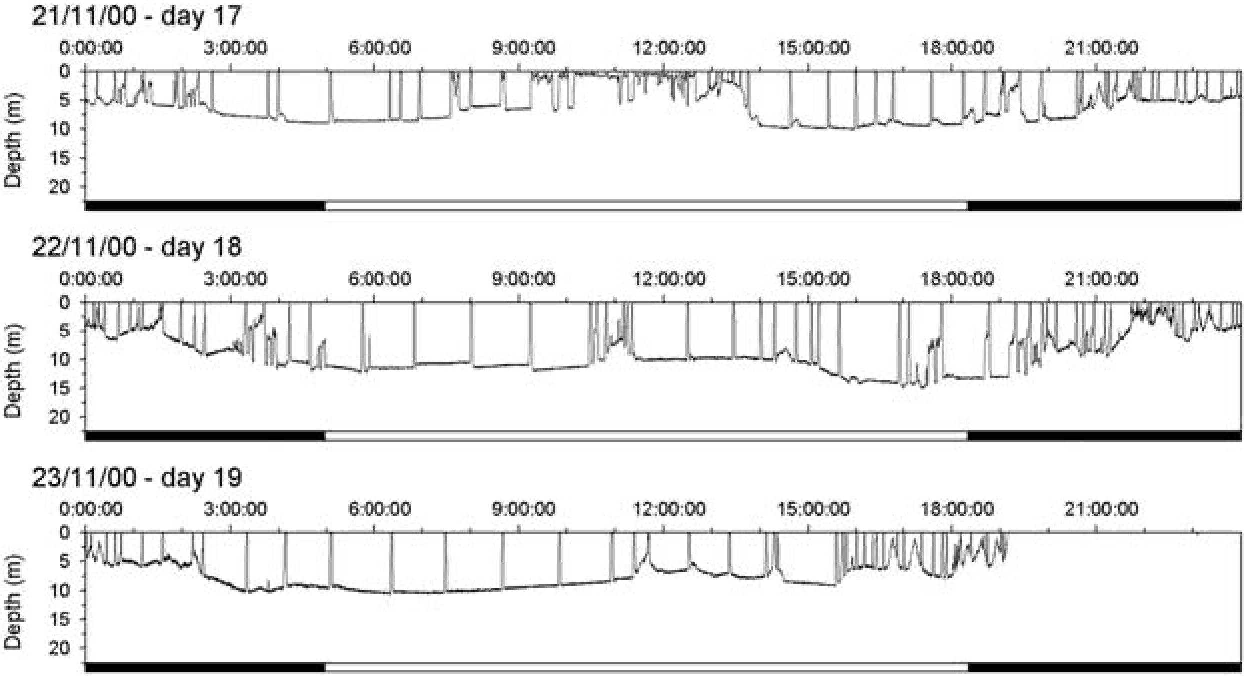


Figure 2 continued. The full dive profile of turtle T97213 from Curtis Island. The bar along the bottom signifies day and night, with the open bar being from sunrise to sunset, and the black bar from sunset to sunrise.

at Bare Sand Island had longer gradual ascent dives (Table 1), i.e. dive types 3, 4, s4 and d4 ($P=0.007$, power of test 0.792, *t*-test). Dives of type 4 were especially long in the Bare Sand Island turtles ($P=0.003$, *t*-test), where the depth and duration were similar to dive type 1a in any one individual.

Turtles at Bare Sand Island showed a stronger correlation between the mean dive depth and duration of dives of type 1a (Fig. 5 a and b) than turtles at Curtis Island, with correlations varying extensively within both populations. For both populations the correlations between mean depth and dive durations were greater for dives of type 3, 4, s4 and d4 (Fig. 5 c and d). Average dive duration for dive type 1 was not correlated to the size, i.e. CCL, of the turtles, after removing the effect of depth (partial regression).

Only some turtles showed a correlation between the dive duration of type 1a dives and the surface duration before and/or after the dive (maximum r^2 were 0.35 and 0.42 for pre- and post-dive surface duration, respectively, $P<0.001$, least square linear regressions) (Fig. 6).

Diel patterns of behaviour

Most turtles showed some preference for dive type 1a during the day, and gradual ascent dives, in particular dive type 4, during the night. The dives were divided into those starting at night and those starting during the day, where night and day was determined by the official sunset and sunrise times for the location of the nesting beach for each day. Turtles at both sites spent on average 14% more time engaged in dive type 1a during the day compared to the night. On average, 6% of the time was spent engaged in dives of either type 3, 4, s4 or d4 during the day, and 15% at night, with great variations between individuals.

Patterns of behaviour throughout the internesting interval

Early and late in the internesting interval there were short and presumably active dives, while dives of type 1a were more prevalent in the approximate middle third of the interval (Fig. 7). Also, the diel pattern described above was more common at this time; e.g. turtle K26302 showed a strong diel pattern on days 4–9, but not on other days. The turtles at Curtis Island engaged dominantly in dives of type 1a from day 5 and prior to the 3 days before next nesting. Similarly, at Bare Sand Island the turtles predominantly engaged in dives of type 1a from day 6 and prior to 4 days before the next nesting event. For the latter population this meant that dive type 1a was significantly more frequent during egg maturation (day 3 to 9) and least frequent during the first 36 hours, i.e. prior to ovulation, of the internesting interval (relative occurrence of dive type 1a between 0-36 h and 72-216 h into the internesting interval, $P<0.001$, *t*-test). None of the turtles had more than a few short dives of type 1a the day before the next nesting event. Instead, the last three or four days in both populations were spent close to the surface (Fig. 7), consistent with turtles staying in shallow water close to the nesting beach. Dives of type 2 and 5, which were otherwise uncommon, occurred more frequently at the end of the interval.

The depth to which turtles dived also changed during the course of the internesting interval (Fig. 3). Six of the ten Curtis Island turtles quickly reached deep water after leaving the beach, then after three days appeared to stay in shallower water until a few days prior to the next nesting event. They then dived deeper again until shortly before next nesting event when they apparently returned closer to land. A different depth pattern was evident in most Bare Sand Island turtles, where the first and last few days were spent at much shallower depths than for the rest of the internesting interval (Fig. 3 b).

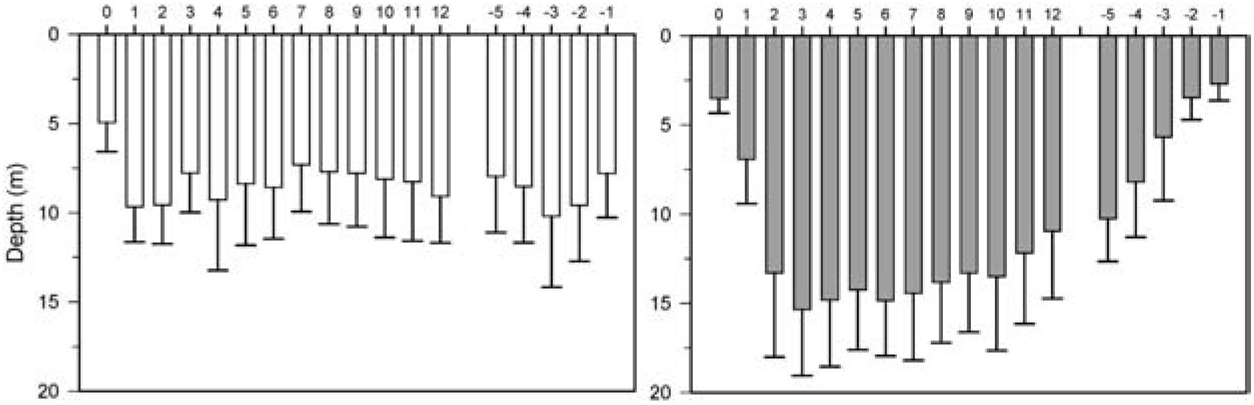


Figure 3. The mean depth with one standard deviation throughout the internesting interval for *N. depressus,* from Curtis Island (left) and Bare Sand Island (right). Day 0 indicates the time prior to midnight on the night recording started and hence only includes turtles that nested prior to midnight. Day 5 indicates five days after last nesting, while -5 indicates 5 days before next nesting event.

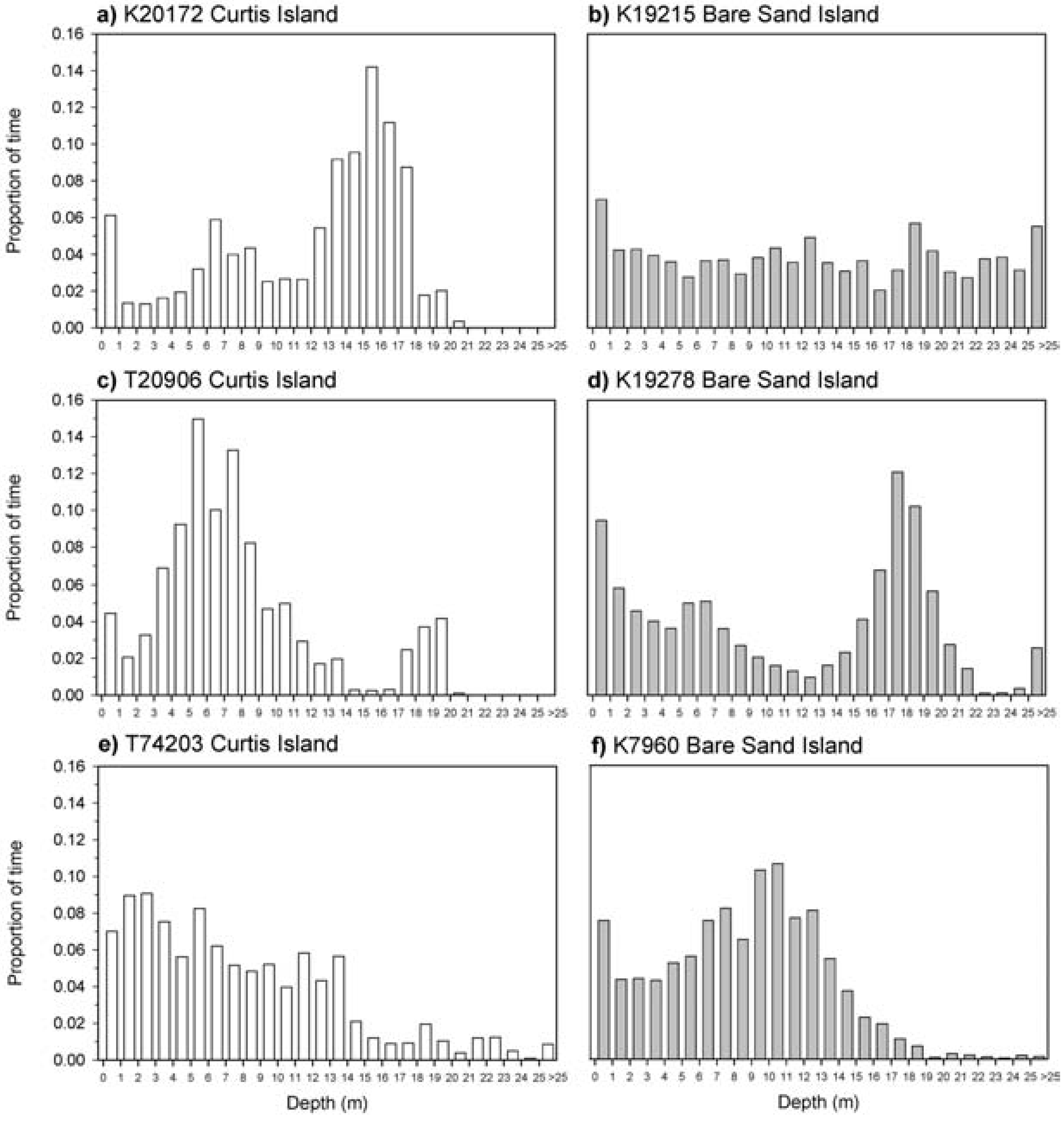


Figure 4. The depth distribution in three *N. depressus,* from Curtis Island (a, c & e) and three from Bare Sand Island (b, d & f), emphasizing the range within the species.

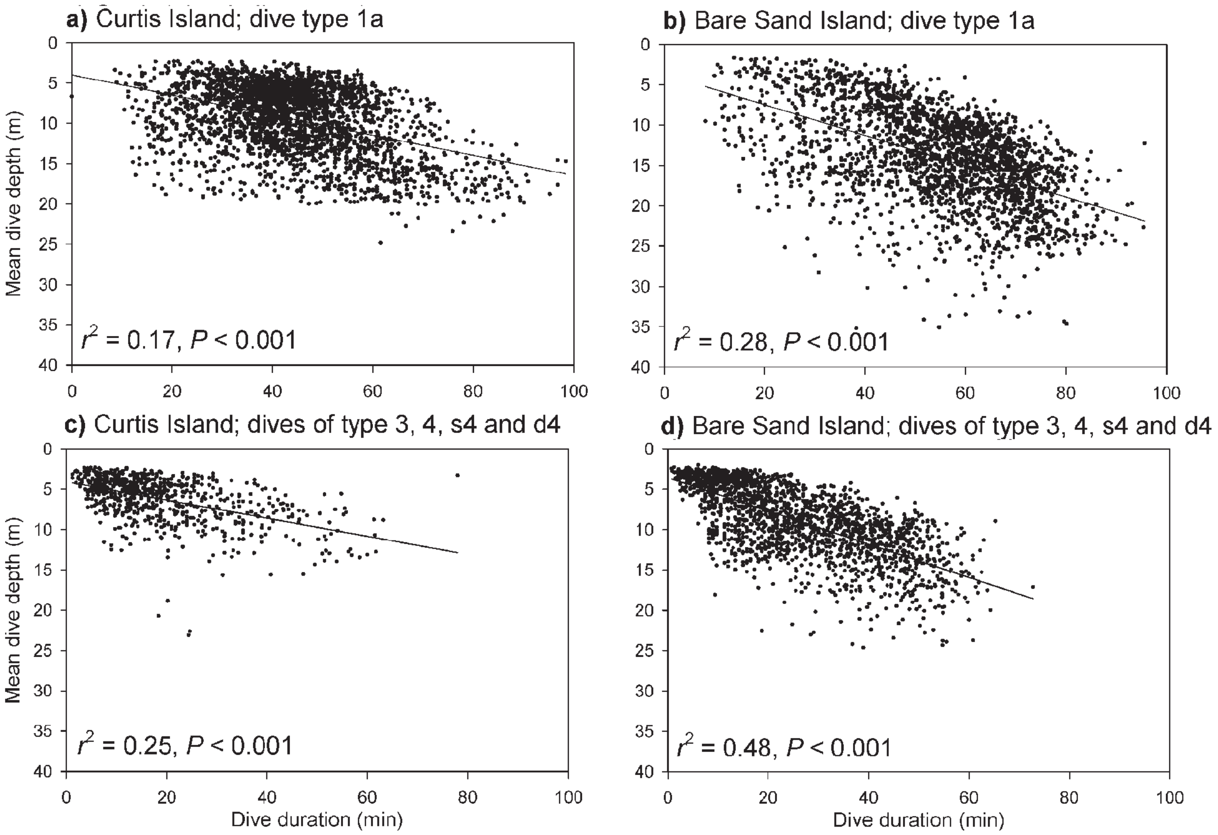


Figure 5. The mean dive depth of a single dive was related to the dive duration of the dive for both dive type 1a (a and b) and all dive types 3, 4, s4 and d4 (c and d) for turtles nesting at both Curtis Island (a and c) and Bare Sand Island (b and d). All turtles from each site are included, and the lines indicate linear regressions (least squares).

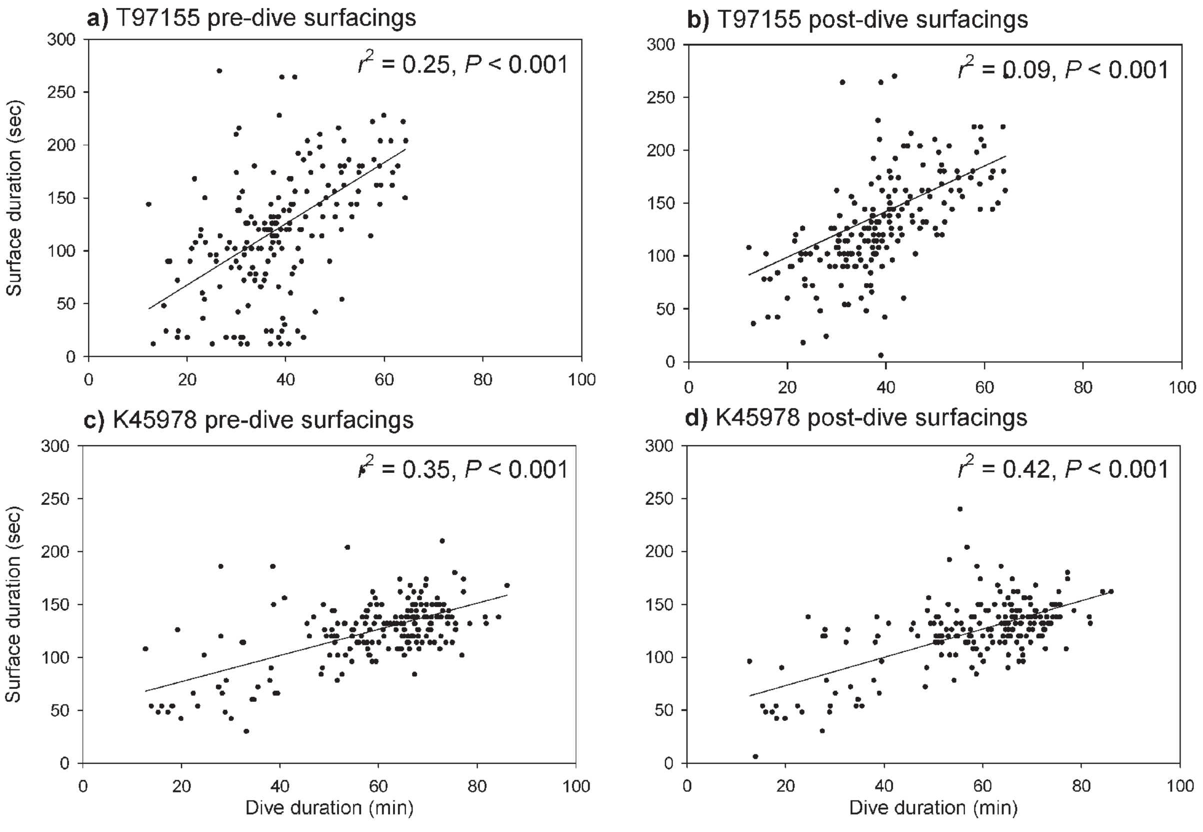


Figure 6. The time spent at the surface before and after dive type 1a was in some individuals correlated to the duration of the dive. Two examples are shown: T97155 had the median correlation coefficient for the post-dive surfacing events (b), and the next highest of any turtle for pre-dive surfacing events (a). K45978 had the maximum correlation found in any individual turtle for both pre- and post-dive surfacing events (c and d).

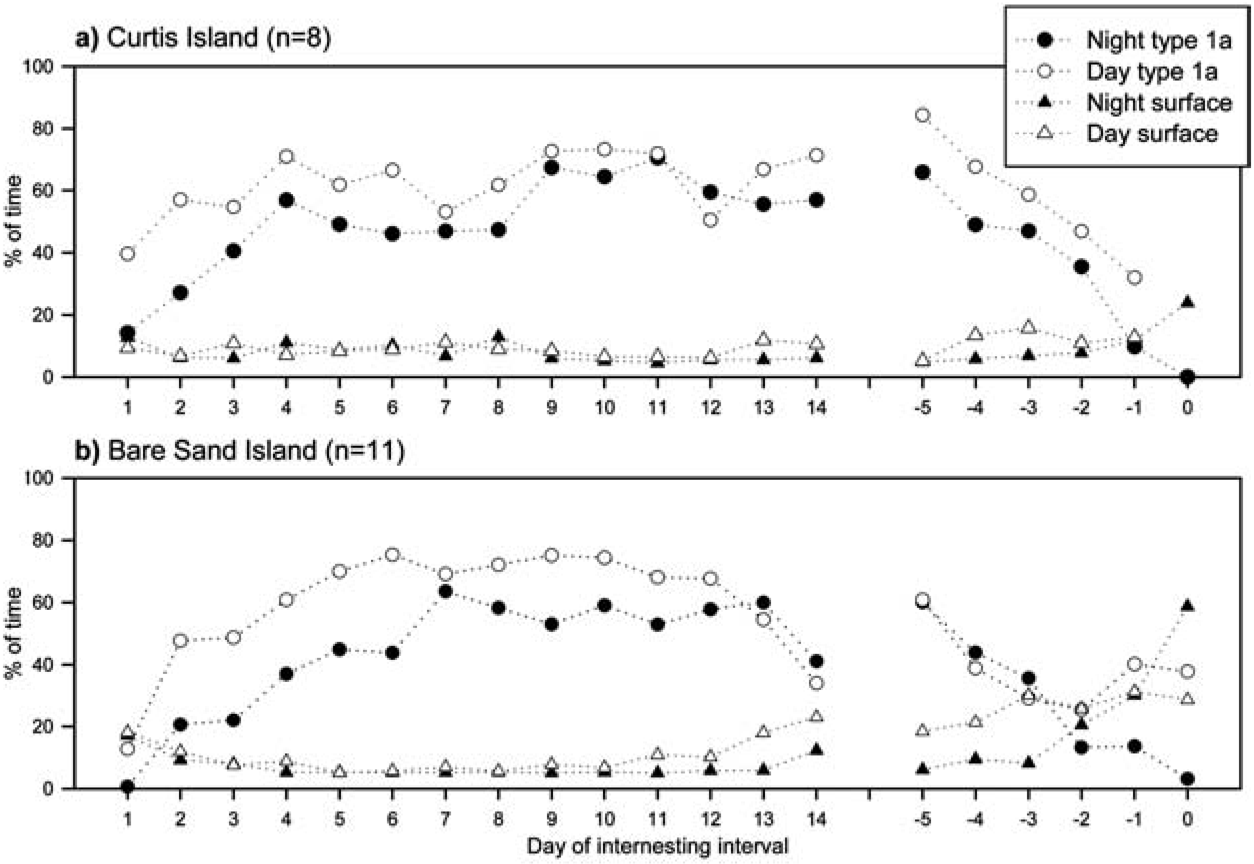


Figure 7. Time spent engaged in dive type 1a during the day and night over the cause of the internesting interval at Curtis Island (a) and Bare Sand Island (b). The Curtis Island data-set excludes the two turtles where data was not obtained from the entire internesting interval (a). Day 1 includes data from the night the turtles nested and the following day. Day 5 indicates five days after last nesting, while -5 indicates 5 days before next nesting event.

Discussion

The results in the present study support the idea that a sea turtle is a 'surfacing' animal rather than a 'diving' animal (Kramer 1988), with time spent at the surface negligible and time spent at shallow depth limited. This suggests that neither population of *N. depressus* increases body temperature by basking, not between nesting attempts anyway and neither do they appear to spend much time resting at the surface. Perhaps it was other life stages or turtles at other nesting beaches that gave rise to the published impression that this species often 'basks' (Cogger and Lindner 1969; Bustard 1972).

The accepted view that voluntary submergences by turtles are fully aerobic (Lutz and Bentley 1985; Hochscheid *et al.* 2005) is also supported. Surface time after even the longest dives was at most a few minutes, which would not be long enough to recover from build-up of lactic acid (Berkson 1967; Lutz and Bentley 1985). Replenishing the oxygen store apparently takes a little longer after a long dive, however, as suggested by the correlation between the durations of type 1a dives and time at the surface (Fig. 6). This has been reported in other sea turtles also (*C. caretta*: Lutcavage and Lutz 1991; *C. mydas*: West *et al.* 1992; *D. coriacea*: Reina *et al.* 2005; Wallace *et al.* 2005).

The most common dive type among the turtles was type 1a, as commonly found in studies on other internesting sea turtles (Hays et *al.* 1999; 2002b; Hochscheid et *al.* 1999; Starbird *et al.* 1999; Houghton *et al.* 2002). The turtles probably remained relatively still on the seafloor during these dives. The records show fluctuations in depth which reflect tidal rise and fall, and even though *N. depressus* prefers flat soft-bottomed habitat (Limpus *et al.* 1983) on which movements could be made without changing depth, dives of type 1a were also generally the longest of all dives, adding weight to the conclusion that they are spent resting. Many individuals also showed a significant correlation between the depth and duration of dives of type 1a, which is to be expected if the metabolic rate is similar between dives. Type 1b dives, on the other hand, showed vertical movements not associated with the tidal rise and fall, and these may be associated with turtles moving on the sea floor. Charts suggests that the Curtis Island population may experience more variable bathymetry (Sperling 2007), where dive type 1b was also almost twice as common compared to Bare Sand Island.

Without more detailed information the exact nature of these dive patterns is uncertain but some speculations can be made. The gradual ascent dives, i.e. dives of type 3, 4, s4 and d4, are likely to be dives used when moving around, the gradually ascending phase being associated with energy conservation as suggested previously in *C. mydas* and *C. caretta* (Hochscheid *et al.* 1999; Houghton *et al.* 2002). This interpretation is supported by the positive correlation between depth and duration (Fig. 5). Gradual ascent dives were more common at Bare Sand Island, which may be due to the deeper bathymetry there. In deeper water these dives may be favoured over dives to the seafloor as a way to conserve energy, exemplified by dive type s4, which is likely to be relatively active compared to type 4 and d4 (Sperling 2008) and was more common at Bare Sand Island. These dives may be favoured over dives to the seafloor in deeper water, and may perhaps serve as exploratory dives, while dive type 1b, twice as common at Curtis Island, may serve the same explorative purpose in shallower water.

Similar studies on other species of sea turtles have reported data from one or a few individuals (Eckert *et al.* 1986; 1996; Sakamoto *et al.* 1990a; 1993; Hochscheid *et al.* 1999; Houghton *et al.* 2002). In our study, although the dives could be categorized relatively easily, the proportional occurrence of the different types varied extensively between individuals, showing that data collected from small sample sizes should be treated cautiously.

Dive durations were often longer than one hour, with dives of up to 1.5 h common in several individuals. These exceed dive times reported in other larger sea turtles (*C. caretta*: Sakamoto *et al.* 1990a; 1993; Houghton *et al.* 2002; Sperling 2007; *D. coriacea*: Eckert *et al.* 1986; Reina *et al.* 2005; Wallace *et al.* 2005; *C. mydas*; Hays *et al.* 2000) with means comparable to the durations reported in the smaller *L. olivacea* (Plotkin 1994) and *E .imbricata* (Starbird *et al.* 1999) and captive *C. caretta* (Hochscheid *et al.* 2003). Longer dives seen in the present study concur with the observations on fishing trawlers, that *N. depressus* survive forced submersion better than other sea turtles (Poiner *et al.* 1990; Poiner and Harris 1996). Sea turtles are known to have a very efficient oxygen storage and transport system (Lutcavage and Lutz 1997) and this may be especially well developed in *N. depressus* through their having oxygen carrying capacity at the high end for diving reptiles and a higher oxygen affinity than *C. caretta* (Sperling *et al.* 2007). They may be specialised for long dives in shallow water (Sperling *et al.* 2007).

While type 1a dives occurred to a variety of depths for the two populations of *N. depressus*, it is interesting to note that they had comparable maximum durations despite an almost 10 min difference in mean dive duration. Although the greater depths available to the Bare Sand Island turtles implies more time spent travelling to and from the surface, the descent and ascent usually lasted only between 1 and 3 min. The comparable maximum duration may therefore suggest an upper limit to *N. depressus* diving capability, regardless of the bathymetry encountered. CCL did not affect the duration of dive type 1a. The maximum depth of 44 m recorded fall within *N. depressus* known maximum dive depth of 40-45 m (Walker 1991; Poiner and Harris 1996; Robins and Mayer 1998). However, the depths recorded here are most likely a result of the depth available within the internesting area, rather than a physiological maximum. Temperature is not likely to have affected dive performance in the present study as there was only a negligible 0.6 °C difference between the water temperature at the two study sites (Sperling 2007).

The slightly higher occurrence type 1a dives during the day compared to the night (by 0 to 28%) is in contrast to what was found in *C. mydas* from Ascension Island (Hays *et al.* 2002b) and in *C. caretta* in Queensland (Sperling 2007). Reported diel patterns in sea turtles often include a change in depth, commonly with shallower dives during the day and deeper dives at night (Sakamoto *et al.* 1990a; 1993; Eckert 2002), suggesting a change of habitat between day and night. No consistent diel pattern was found between occupancy of different depths in either of the two populations. However, in at least some of the individuals there appear to be a preference for spending time in mid-water during the night and the sea floor during the day.

Type 1a dives also occurred more frequently in the approximate middle third of the internesting interval, in agreement with a study on internesting *E. imbricata* which showed less activity on days 2-12 (Starbird *et al.* 1999). Shallow dives, on the other hand, were especially frequent early and late in the internesting interval when the turtles may travel to and from the internesting habitat. Making only shallow dives when travelling is consistent with the general idea that turtles should travel at a depth of two to three times an animal's body diameter in order to reduce drag (Williams 1989; Houghton *et al.* 2002). The interpretation of travelling for several days before the next nesting event is also consistent with telemetry data on the same populations, where the turtles were known to be in close proximity to the nesting beach for the last few days before nesting (Sperling 2007). Similarly, *C. mydas* and *C. caretta* have been shown to spend more time at or near the surface as the nesting date approaches (Hays *et al.* 1991; 1999). The relatively inactive middle period of the internesting interval coincides approximately with the time of egg maturation between day 3 and day 9 (Miller 1985). Tucker *et al.* (1995) suggested that the changes in movement observed over the internesting interval in a population of *C. caretta* may be associated with the physiological process of egg development. In the freshwater turtle *Pseudemydura umbrina,* ovulation is a sensitive time which can be disrupted by the stress of capture (Kuchling and Bradshaw 1993). Perhaps a similar sensitive period exists in sea turtles, which would explain their apparent inactivity for long periods on the seafloor following ovulation.

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References

Berkson, H. 1967. Physiological adjustments to deep diving in the Pacific green turtle (Chelonia mydas agassizii). *Comparative Biochemical Physiology* **21**: 507-524.

Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. *Copeia* **1985(3)**: 736-751.

Brill, R.W., Balazs, G.H., Holland, K.N., Chang, R.K.C., Sullivan, S. and George, J.C. 1995. Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (Chelonia mydas L) within a foraging area in the Hawaiian Islands. *Journal of Experimental Marine Biology and Ecology* **185**: 203-218.

Brischoux, F., Boonet, X., Cook, T.R. and Shine, R. 2008. Allometry of diving capacities: ectothermy vs endothermy. *Journal of Evolutionary Biology* **21**: 324-329.

Bustard, R. 1972. The flatback. Pp. 74-88 in Australian Sea Turtles, edited by R. Bustard. Collins, Glasgow.

Carr, A., Ross, P. and Carr, S. 1974. Internesting behavior of the green turtle, Chelonia mydas, at a mid-ocean island breeding ground. *Copeia* **1974**: 703-706.

Cogger, H.G. and Lindner, D.A. 1969. Marine turtles in northern Australia. *Australian Zoologist* **15**: 150-159.

Dutton, P., Broderick, D. and FitzSimmons, N. 2002. Defining management units: molecular genetics. Pp. 93-101 in Proceedings of the Western Pacific Sea Turtle Cooperative Research & Management Workshop, edited by I. Kinan. Western Pacific Regional Fishery Management Council, Honolulu, USA.

Eckert, S.A. 2002. Swim speed and movement patterns of gravid leatherback sea turtles (Dermochelys coriacea) at St Croix, US Virgin Islands. *Journal of Experimental Biology* **205**: 3689-3697.

Eckert, S.A., Nellis, D.W., Eckert, K.L. and Kooyman, G.L. 1986. Diving patterns of two leatherback sea turtles (Dermochelys coriacea) during internesting intervals at Sandy Point, St. Criox, U.S. Virgin Islands. *Herpetologica* **42**: 381-388.

Eckert, S.A., Liew, H.C., Eckert, K.L. and Chan, E.H. 1996. Shallow water diving by leatherback turtles in the South China Sea. *Chelonian Conservation and Biology* **2**: 237-243.

Graham, J.B., Gee, J.H., Motta, J. and Rubinoff, I. 1987. Subsurface buoyancy regulation by the sea snake Pelamis platurus. *Physiological Zoology* **60**: 251-261.

Guinea, M.L. 1994. A possible model to explain winter nesting by the flatback turtle, Natator depressus at Fog Bay, Northern Territory. Pp 154-155 in Proceedings of the Australian Marine Turtle Conservation Workshop, edited by R. James. Queensland department of Environment and Heritage, Australian Nature Conservation Agency, Gold Coast.

Hays, G.C., Webb, P.I., Hayes, J.P., Priede, I.G. and French, J. 1991. Satellite tracking of a loggerhead turtle (Caretta caretta) in the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom* **71**: 743-746.

Hays, G.C., Luschi, P., Papi, F., del Seppia, C. and Marsh, R. 1999. Changes in behaviour during the inter-nesting period and post-nesting migration for Ascension Island green turtles. *Marine Ecology Progress Series* **189**: 263-273.

Hays, G.C., Adams, C.R., Broderick, A.C., Godley, B.J., Lucas, D.J., Metcalfe, J.D. and Prior, A.A. 2000a. The diving behaviour of green turtles at Ascension Island. *Animal Behaviour* **59**: 577-586.

Hays, G.C., Akesson, S., Broderick, A.C., Glen, F., Godley, B.J., Luschi, P., Martin, C., Metcalfe, J.D. and Papi F. 2001. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *Journal of Experimental Biology* **204**: 4093-4098.

Hays, G.C., Broderick, A.C., Glen, F. and Godley, B.J. 2002a. Change in body mass associated with long-term fasting in a marine reptile: the case of green turtles (Chelonia mydas) at Ascension Island. *Canadian Journal of Zoology* **80**: 1299-1302.

Hays, G.C., Glen, F., Broderick, A.C., Godley, B.J. and Metcalfe, J.D. 2002b. Behavioural plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtle (Chelonia mydas) populations. *Marine Biology* **141**: 985-990.

Hays, G.C., Metcalfe, J.D., Walne, A.W. and Wilson, R.P. 2004. First records of flipper beat frequency during sea turtle diving. *Journal of Experimental Marine Biology and Ecology* **303**: 243-260.

Hirth, H.F. 1980. Some aspects of the nesting behaviour and reproductive biology of sea turtles. *American Zoologist* **20**: 507-523.

Hochscheid, S., Godley, B.J., Broderick, A.C. and Wilson, R.P. 1999. Reptilian diving: highly variable dive patterns in the green turtle Chelonia mydas. *Marine Ecology Progress Series* **185**: 101-112.

Hochscheid, S., Bentivegna, F. and Speakman, J.R. 2003. The dual function of the lung in chelonian sea turtles: buoyancy control and oxygen storage. *Journal of Experimental Marine Biology and Ecology* **297**: 123-140.

Hochscheid, S., Bentivegna, F. and Hays, G.C. 2005. First records of dive durations for a hibernating sea turtle. *Biology Letters* **1**: 82-86.

Houghton, J.D.R., Broderick, A.C., Godley, B.J., Metcalfe, J.D. and Hays, G.C. 2002. Diving behaviour during the internesting interval for loggerhead turtles Caretta caretta nesting in Cyprus. *Marine Ecology Progress Series* **227**: 63-70.

Kramer, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Canadian Journal of Zoology* **66**: 89-94.

Kuchling, G. and Bradshaw, S.D. 1993. Ovarian cycle and egg production of the western swamp tortoise Pseudemydura umbrina (Testudines: Chelidae) in the wild and in captivity. *Journal of Zoology* **229**: 405-419.

Limpus, C.J. 1971. The flatback turtle, Natator depressa Garman in SE Queensland, Australia. *Herpetologica* **27**: 431-446.

Limpus, C.J. 1985. *A Study of the Loggerhead Sea Turtle, Caretta caretta, in Eastern Australia.* Ph.D. dissertation. The University of Queensland, Brisbane.

Limpus, C.J., Parmenter, C.J., Baker, V. and Fleay, A. 1983. The flatback turtle, Chelonia depressa, in Queensland: post-nesting migration and feeding ground distribution. *Australian Wildlife Research* **10**: 557-561.

Limpus, C.J., Fleay, A. and Baker, V. 1984. The flatback turtle, Chelonia depressa, in Queensland (Australia): Reproductive periodicity, philopatry and recruitment. *Australian Wildlife Research* **11**: 579-588.

Limpus, C.J., Gyuris, E. and Miller, J.D. 1988. Reassessment of the taxonomic status of the sea turtle genus Natator McCulloch, 1908, with a redescription of the genus and species. *Transactions of the Royal Society of South Australia* **112**: 1-10.

Limpus, C.J., Couper, P.J. and Couper, K.L.D. 1993. Crab Island revisited: Reassessment of the world's largest flatback turtle rookery after twelve years. *Memoirs of the Queensland Museum* **33**: 277-289.

Limpus, C.J., Miller, J.D. and Preece, N. 1994. The basking greens of Bountiful Island Kay's turtles revisited. NOAA Technical Memorandum NMFS-SEFSC-351; 76-77.

Limpus, C.J., De Villiers, D.L., De Villiers, M.A., Limpus, D.J. and Read, M. 2001. The loggerhead turtle, Caretta caretta, in Queensland: feeding ecology in warm temperate waters. *Memoirs of the Queensland Museum* **46**: 631-645.

Lutcavage, M.E. and Lutz, P.L. 1991. Voluntary diving metabolism and ventilation in the loggerhead sea turtle. *Journal of Experimental Marine Biology and Ecology* **147**: 287-296.

Lutcavage, M.E. and Lutz, P.L. 1997. Diving physiology. Pp. 277-296 in The Biology of Sea Turtles, edited by P. Lutz and J. Musick. CRC Press, New York.

Lutz, P.L. and Bentley, T.B. 1985. Respiratory physiology of diving in the sea turtle. *Copeia* **1985(3)**: 671-679.

Lutz, P.L. and Musick, J.A. 1997. *The Biology of Sea Turtles*. CRC Press, New York.

Mendonca, M.T. and Pritchard, P.C.H. 1986. Offshore movements of post-nesting Kemp's ridley sea turtles (Lepidochelys kempi). *Herpetologica* **42**: 373-381.

Miller, J.D. 1985. Embryology of Marine Turtles. Pp. 270-328 in *Biology of the Reptilia*, Development A, edited by C. Gans. John Wiley & Sons, New York.

Minamikawa, S., Naito, Y. and Uchida, I. 1997. Buoyancy control in diving behavior of the loggerhead turtle, Caretta caretta. *Journal of Ethology* **15**: 109-118.

Minamikawa, S., Naito, Y., Sato, K., Matsuzawa, Y., Bando, T. and Sakamoto, W. 2000. Maintenance of neutral buoyancy by depth selection in the loggerhead turtle Caretta caretta. *Journal of Experimental Biology* **203**: 2967-2975.

Plotkin, P.T. 1994. *The Migratory and Reproductive Behavior of the Olive Ridley, Lepidochelys olivacea (Eschscholtz, 1829) in the Eastern Pacific Ocean*. Ph.D. dissertation, Texas A&M University, Texas.

Poiner, I.R., Buckworth, R.C. and Harris, A.N.M. 1990. Incidental capture and mortality of sea turtles in Australia's northern prawn fishery. *Australian Journal of Marine and Freshwater Research* **41**: 97-110.

Poiner, I.R. and Harris, A.N.M. 1996. Incidental capture, direct mortality and delayed mortality of sea turtles in Australia's Northern Prawn Fishery. *Marine Biology* **125**: 813-825.

Read, M.A., Grigg, G.C. and Limpus, C.J. 1996. Body temperatures and winter feeding in immature green turtles, Chelonia mydas, in Moreton Bay, southeastern Queensland. *Journal of Herpetology* **30**: 262-265.

Reina, R.D., Abernathy, K.J., Marshall, G.J. and Spotila, J.R. 2005. Respiratory frequency, dive behaviour and social interactions of leatherback turtles, Dermochelys coriacea during the inter-nesting interval. *Journal of Experimental Marine Biology and Ecology* **316**: 1-16.

Robins, J.B. and Mayer, D.G. 1998. Monitoring the impact of trawling on sea turtle populations of the Queensland east coast. Queensland Department of primary industries project report series No. Q098012.

Rubinoff, I., Graham, J.B. and Motta, J. 1986. Diving of the sea snake Pelamis platurus in the Gulf of Panama I. Dive depth and duration. *Marine Biology* **91**: 181-191.

Sakamoto, W., Naito, Y., Uchida, I. and Kureha, K. 1990a. Circadian rhythm on diving motion of the loggerhead turtle Caretta caretta during inter-nesting and its fluctuations induced by the oceanic environmental events. *Nippon Suisan Gakkaishi* **56**: 263-272.

Sakamoto, W., Uchida, I., Naito, Y., Kureha, K., Tujimura, M. and Sato, K. 1990b. Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* **56**: 1435-1443.

Sakamoto, W., Sato, K., Tanaka, H. and Naito, Y. 1993. Diving patterns and swimming environment of two loggerhead turtles during internesting. *Nippon Suisan Gakkaishi* **59**: 1129-1137.

Sapsford, C.W. and van der Riet, M. 1979. Uptake of solar radiation by the sea turtle, Caretta caretta, during voluntary surface basking. *Comparative Biochemistry and Physiology A* **63**: 471-474.

Sato, K., Sakamoto, W., Matsuzawa, Y., Tanaka, H., Minamikawa, S. and Naito, Y. 1995. Body-temperature independence of solar-radiation in free- ranging loggerhead turtles, Caretta caretta, during internesting periods. *Marine Biology* **123**: 197-205.

Sperling, J.B. 2007. *The Behaviour and Physiology of the Flatback Turtle (Natator depressus)*. PhD dissertation, The University of Queensland, Brisbane.

Sperling, J.B. 2008. Two new dive types with a gradual ascent phase in flatback turtles (Natator depressus). *Marine Turtle Newsletter* **120**: 9-11.

Sperling, J.B. and Guinea, M.L. 2004. Harness for attachment of satellite transmitters on flatback turtles. *Marine Turtle Newsletter* **103**: 11-13.

Sperling, J.B., Grigg, G.C., Beard, L.B. and Limpus, C.J. 2007. Respiratory properties of blood in flatback turtles (Natator depressus). *Journal of Comparative Physiology B* **177**: 779-786.

Starbird, C.H., Hillis-Starr, Z., Harvey, J.T. and Eckert, S.A. 1999. Internesting movements and behavior of hawksbill turtles (Eretmochelys imbricata) around Buck Island Reef National Monument, St. Criox, U.S. Virgin Island. *Chelonian Conservation and Biology* **3**: 237-243.

Tanaka, H., Sato, K., Matsuzawa, Y., Sakamoto, W., Naito, Y. and Kuroyanagi, K. 1995. Analysis of possibility of feeding of loggerhead turtles during internesting periods based on stomach temperature measurements. *Nippon Suisan Gakkaishi* **61**: 339-345.

Tucker, A.D., Fitzsimmons, N.N. and Limpus, C.J. 1995. Conservation implications on internesting habitat use by loggerhead turtles Caretta caretta in Woongarra Marine Park, Queensland, Australia. *Pacific Conservation Biology* **2**: 157-166.

Van Dam, R.P. and Diez, C.E. 1997. Diving behaviour of immature hawksbill turtles (Eretmochelys imbricata) in a Caribbean reef habitat. *Coral Reefs* **16**: 133-138.

Walker, T.A. 1991. Juvenile flatback turtles in proximity to coastal nesting islands in the Great Barrier Reef province. *Journal of Herpetology* **25**: 246-248.

Walker, T.A. and Parmenter, C.J. 1990. Absence of a pelagic phase in the life cycle of the flatback turtle, Natator depressa (Garman). *Journal of Biogeography* **17**: 275-278.

Wallace, B.P., Williams, C.L., Paladino, F.V., Morreale, S.J., Lindstrom, R.T. and Spotila, J.R. 2005. Bioenergetics and diving activity of internesting leatherback turtles Dermochelys coriacea at Parque Nacional Marino las Baulas, Costa Rica. *Journal of Experimental Biology* **208**: 3873-3884.

West, N.H., Butler, P.J. and Bevan, R.M. 1992. Pulmonary blood flow at rest and during swimming in the green turtle, Chelonia mydas. *Physiological Zoology* **65**: 287-310.

Whiting, S.D. and Guinea, M.L. 2006. The nesting biology of flatback turtles in the tropics: Seven years of surveys on Bare Sand Island, Darwin, Northern Territory, Australia. P. 159 in Proceedings of the twenty-third annual symposium on sea turtle biology and conservation, compiled by N.J. Pilcher. NOAA Technical Memorandum NMFS-SEFSC-536.

Whittow, G.H. and Balazs, G.H. 1982. Basking behaviour of the Hawaiian green turtle (Chelonia mydas). *Pacific Science* **36**: 129-139.

Williams, T.M. 1989. Swimming by sea otters: adaptations for low energetic cost locomotion. *Journal of Comparative Physiology* **164**: 815-824.

APPENDIX I

A final check of the harness on a *Natator depressus*, with a satellite transmitter and a Time-Depth Recorder attached. The instruments will obtain information on the location and diving performance of the turtle while it is preparing the next cluth of eggs, which it will lay about two weeks later at the same Bare Sand Island nesting beach.

Photo, Manuel Schoonveld

Two *Natator depressus* are leaving the nesting beach at Bare Sand Island after having a satellite transmitter and a Time-Depth Recorder attached using a specially designed harness.

Photo, Manuel Schoonveld

A *Natator depressus* is leaving the nesting beach at Bare Sand island after having laid a clutch of eggs, and will be away for about two weeks before returning to the same beach to lay another clutch.

Photo, Jannie Bech Sperling

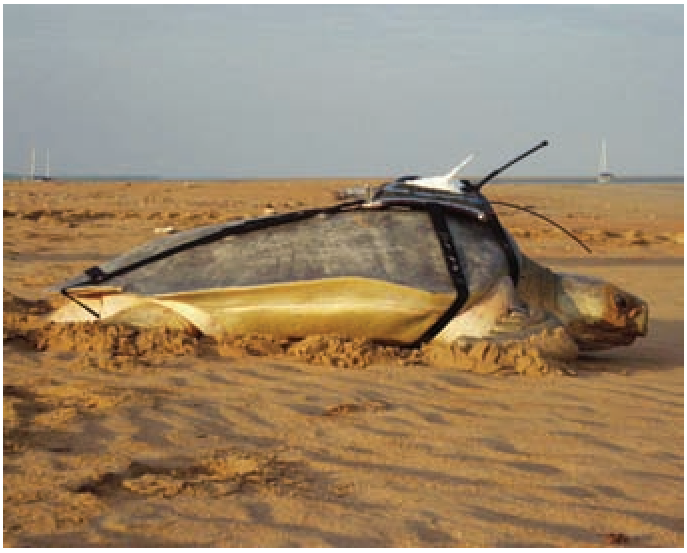
APPENDIX I

A *Natator depressus* is crawling back to the water at Bare Sand Island nesting beach after having laid a clutch of eggs. With a specially designed harness containing a satellite transmitter and a Time-Depth Recorder, data on the turtles' movements and dive performance is recorded while it is preparing the next clutch off eggs.

Photo, Jannie Bech Sperling

A *Natator depressus* shortly after leaving the Bare Sand Island nesting beach with a harness, containing a satellite transmitter and a Time-Depth Recorder, attached.

Photo, Jannie Bech Sperling



A *Natator depressus* is crawling back to the water at Bare Sand Island nesting beach after having laid a clutch of eggs. With a specially designed harness containing a satellite transmitter and a Time-Depth Recorder, data on the turtles' movements and dive performance is recorded while it is preparing the next clutch off eggs.

Photo, Manuel Schoonveld.